

FOUR NEW SPECIES OF CAMBARINCOLIDS  
(CLITELLATA: BRANCHIOBDELLIDA) FROM THE  
SOUTHEASTERN UNITED STATES WITH A  
REDESCRIPTION OF *OEDIPODRILUS MACBAINI*  
(HOLT, 1955)

Perry C. Holt

*Abstract.* — Four new species of cambarincolid branchiobdellidans, *Cambarincola bobbi* from Virginia, *Ellisodrilus carronamus* and *Oedipodrilus anisognathus* from Tennessee, and *Sathodrilus rivigeae* from Arkansas are newly described. In addition, *Oedipodrilus macbaini* (Holt, 1955) is redescribed. Relationships and distributions are discussed.

When the branchiobdellidan collections belonging to the Virginia Polytechnic Institute and State University were given to the National Museum of Natural History of the Smithsonian Institution in the Spring of 1986, I retained in my possession as a loan certain collections from the southeastern United States, including all the material from Tennessee, which I knew to contain a number of new species. This opportunity is taken to describe four of these species and to more fully describe *Oedipodrilus macbaini* (Holt, 1955).

The region composed of the southern Appalachians and associated uplands (the Piedmont and the Interior Low Plateaus) and the Ozark Mountains contains the most diverse branchiobdellidan fauna known for any similarly sized region in the world and may include the original home of the order. An understanding of the relationships and history of the branchiobdellidans awaits a fuller description of this fauna.

Some discussion of generalities and generic and familial diagnoses may be found in Holt (1986). Herein, the intent is merely to describe new species with minimal emphasis placed on any other questions.

*Cambarincola bobbi*, new species  
Fig. 1

*Type specimens.* — Holotype, USNM 101496, four paratypes, USNM 101497–101499, taken on *Cambarus bartonii bartonii* (Fabricius) from a medium-sized stream in Tom's Brook (a town) 5.7 miles south of Strasburg, Shenandoah County, Virginia, by Marvin L. Bobb and Perry C. Holt, 22 Jul 1948.

*Diagnosis.* — Small- to medium-sized worms (holotype 2.2 mm in length); lips obscurely lobed; no oral papillae; dorsal ridges weakly developed; jaws subequal in size, dorsal one slightly larger than ventral one, dark in color, dental formula 5/5; bursa about  $\frac{1}{2}$  to  $\frac{3}{5}$  body diameter in length, elongate ovoid, atrial fold thin, penial sheath about  $\frac{1}{2}$  total length, penis membraneous; spermiducal gland large, length about twice its diameter, no deferent lobes, flexed antero-ventrad at its mid-point; prostate about  $\frac{1}{2}$  length,  $\frac{3}{8}$  diameter of spermiducal gland, differentiated, with large clear ental bulb; spermatheca with prominent ectal duct, bulb ovoid to lanceolate (in optical section), length slightly less than diameter of body.

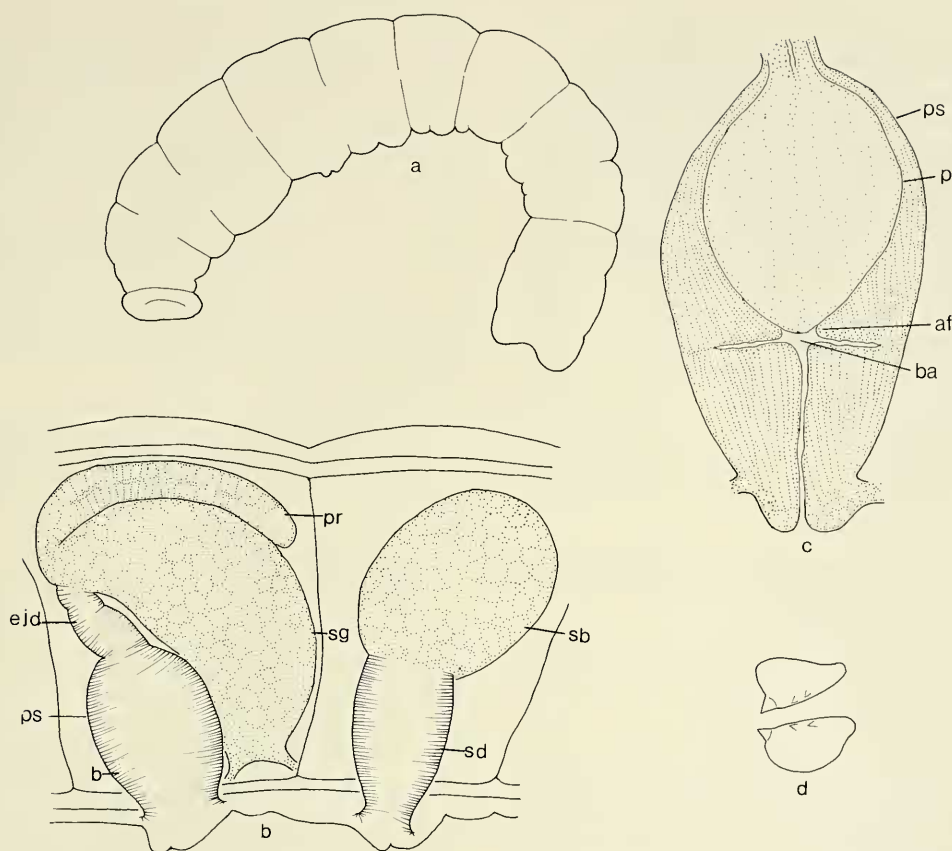


Fig. 1. *Cambarincola bobbi*, holotype. a, Lateral view of entire animal; b, Lateral view of reproductive systems; c, Optical section through bursa and penis; d, Lateral view of jaws. Abbreviations: af, atrial fold; b, bursa; ba, bursal atrium; ejd, ejaculatory duct; p, penis; pr, prostate; ps, penial sheath; sb, spermathecal bulb; sd, spermathecal duct; sg, spermiducal gland.

**Etymology.**—For Dr. Marvin L. Bobb, friend, fellow student, and for a season, field companion.

**Description.**—The five type specimens of *Cambarincola bobbi* have the following mean dimensions: total length, 2.0 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.3 mm.

In external appearance, *C. bobbi* is unremarkable. The lips have four dorsal, two ventral, indistinct lobes. Oral papillae are not detectable, yet there are slight, low undulations of the inner margin of the mouth. The posterior fourth of the head is demar-

cated by a shallow external sulcus and a prominent pharyngeal one. Supernumerary muscles of the dorsal portions of the anterior prosomites of the body segments are poorly developed, thus in profile the body outline is smooth: there are no dorsal ridges. The sucker is prominent and slightly greater in diameter than segment I.

The length of the jaws is about  $\frac{1}{18}$  that of the head; hence, of usual comparative size. The animals available for this study are all strongly bent ventrad. The exact distribution of the teeth, consequently, is difficult to ascertain in most specimens. There is a prominent apical tooth on each jaw with

two small lateral ones flanking it on each side, producing a 5/5 dental formula.

The spermiducal gland is large and reflexed to some extent, often to a right angle, at its mid-length. It has no deferent lobes. The slender prostate is about  $\frac{1}{2}$  the length of the spermiducal gland and is "differentiated," that is, composed of cells less densely granular than those of the spermiducal gland. A large, clear ental bulb is present. The bursa is elongate ovoid in shape. The penis is distinctly less muscular than is usual among members of the genus, consisting of an ovoid sac, presumably protrusible, with a few strands (? muscular) traversing it. The ejaculatory duct is of the usual type, a short muscular tube.

The spermathecal duct is about  $\frac{1}{2}$  the body diameter in length; the bulb is ovoid without an ental process.

*Variations.*—No variations of note, except the extent of reflexion of the spermiducal gland, were detected.

*Affinities.*—*Cambarincola bobbi* clearly belongs to the group of species with a differentiated prostate with an ental bulb that Hoffman (1963:336–341) assigned to his "Philadelphica section" and "group" of the genus. The "Fallax subgroup" in this scheme is distinguished by an equal (and odd) number of teeth borne by each jaw. In this subgroup (consisting of *C. fallax* Hoffman, 1963, and *C. holostomus* Hoffman, 1963), *Cambarincola bobbi* most closely resembles *C. holostomus*.

*Cambarincola holostomus* is described by Hoffman (1963:361) as characterized by an entire peristomium; that is, there is no division of the peristomium into upper and lower lips, a 3/3 dental formula and a "slender elongate, fusiform" spermatheca. In addition to differing from *C. holostomus* in these respects, *C. bobbi* also is distinguished by a larger and more reflexed spermiducal gland and a shorter prostate (Hoffman 1963: 359, fig. 64). *Cambarincola bobbi* resembles *C. fallax* in these features and the 5/5 dental formula, but lacks the characteristic elon-

gated peristomial tentacles of *C. fallax* and differs from both in its membranous penis. The structure of the penis of *C. bobbi* seems to reinforce the previously noted similarities between the bursal-penial complex of the genera *Cambarincola* and *Sathodrilus* Holt, 1968a (Holt 1982:254). However, in this case, it is most likely another example of convergence within the order, since the relatives of *C. bobbi* are presumably "advanced" members of the genus (Hoffman 1963:296–297).

*Host.*—*Cambarus bartonii bartonii*.

*Distribution.*—Known only from the type locality. Other similar streams of the Shenandoah River system should harbor this species.

*Material examined.*—The type series.

*Note.*—The tributaries of the New River in western Virginia and eastern West Virginia and the headwaters of the Holston, Roanoke, James, Shenandoah and Potomac rivers contain many similar species of the genus *Cambarincola*. Some specimens from this area are difficult to identify, but *C. bobbi* appears to be clearly distinct from any previously described species, and is another example of the diversity and the incipient speciation in these waters: waters undoubtedly linked by many stream captures in the recent past.

*Ellisodrilus carronamus*, new species

Fig. 2

*Type specimens.*—Holotype, USNM 119539 and two paratypes, USNM 119540–119541, taken on *Orconectes* sp., from Carr Creek, Overton County, Tennessee, about 3.0 miles south of Livingston, Tennessee, on State Highway 42, by Perry C. and Virgie F. Holt, 26 Jul 1961.

*Diagnosis.*—Small worms (holotype 1.95 mm in length); lips entire, no oral papillae; no dorsal ridges; upper jaw slightly longer than lower, dark brown in color, dental formula (?) 5/5; bursa slightly less than  $\frac{1}{2}$  body diameter in dorso-ventral length, antero-



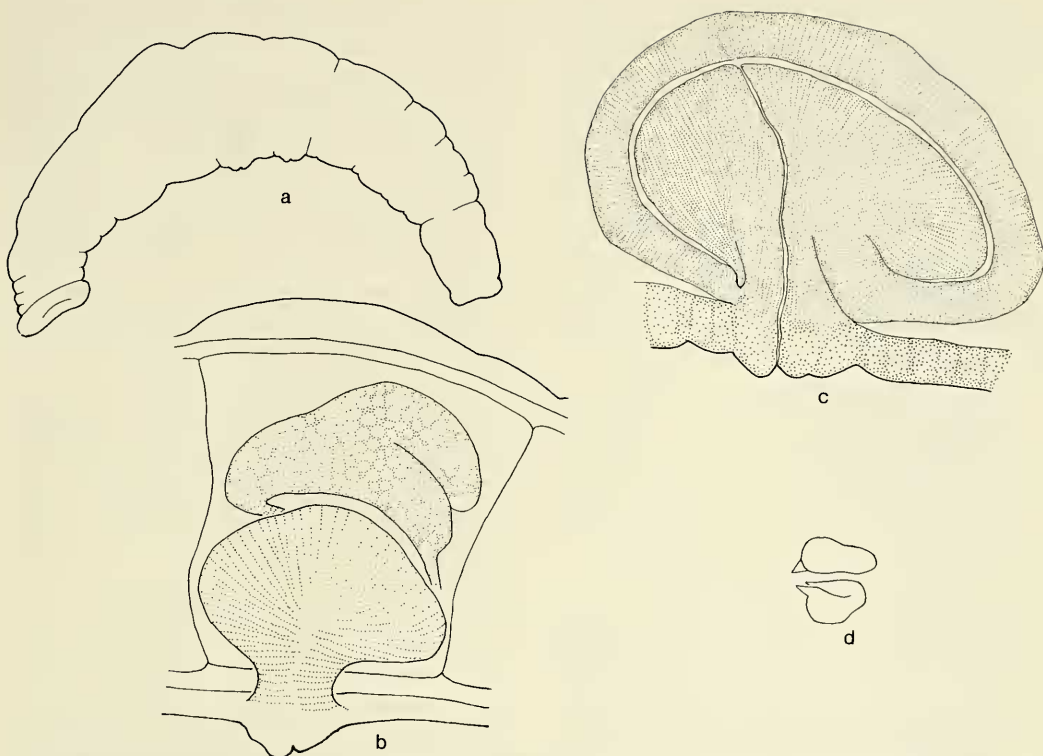


Fig. 2. *Ellisodrilus carronamus*, holotype. a, Lateral view of entire animal; b, Lateral view of male efferent apparatus; c, Optical section of bursa; d, Lateral view of jaws.

posterior dimension (diameter) slightly greater than dorso-ventral one; penis reduced to pore through ental portion of bursa, pseudo-penis formed by enlarged inner-directed atrial fold; ejaculatory duct short, thin; spermiducal gland oriented longitudinally in coelom, lying dorsad to gut, in length about twice its diameter; prostate arises entad to mid-point of spermiducal gland, less than  $\frac{1}{2}$  length, subequal in diameter to latter, non-differentiated, with small ental bulb; no spermatheca.

**Etymology.**—From Greek, *namos*, creek, hence Carr Creek for the type locality and a family that includes friends of my youth for whom the creek was named.

**Description.**—The holotype, which is comparable in size to the other specimens examined, has the following approximate dimensions: total length, 1.9 mm; greatest

diameter, 0.4 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter segment I, 0.2 mm; diameter, sucker, 0.2 mm.

The lips lack lobes; there are no oral papillae. The one internal pharyngeal sulcus has no corresponding external one.

The jaws are brown and prominent, the upper about  $\frac{1}{4}$  the length of the head, the lower somewhat less. No lateral teeth are apparent in the holotype at a magnification of  $500\times$  but some of the paratypes appear to have two lateral teeth at the side of the large median tooth: the dental formula would be, then,  $5/5$ , a point requiring further confirmation.

Dorsal ridges are absent from all segments, but the inter-segmental furrow between VI and VII is deeply incised and the clitellum of segment VII is prominent: this accounts for the greater diameter of segment

VII and gives to this segment a superficial appearance of a dorsal ridge, which, however, entirely lacks supernumerary muscles.

The spermiducal gland, though proportionately large, is unremarkable. There are no obvious deferent lobes and the organ tapers from its greatest diameter at the point of origin of the prostate to its ectal end.

The prostate arises from the spermiducal gland slightly more than  $\frac{1}{3}$  the length of the latter from its ental end and is almost as great in diameter. It is non-differentiated with a small, but distinct, ental bulb.

The bursa is large, filling the ventral half of its segment. Its ectal portion (atrium), which has an inner-directed circular fold (=atrial fold) whose lumen slants towards the postero-dorsal side of the bursa and opens into the bursal cavity opposite the opening of the ejaculatory duct into the atrium, is the most striking feature of the male reproductive system (Fig. 2c). In effect there is no structure which is homologous to the penis of other genera of the branchiobdellidans except the pore formed by the opening of the ejaculatory duct into the lumen of the bursa (atrium). The ejaculatory duct is thin, short and difficult to detect in available material. The atrial fold, a pseudopenis, would appear to be analogous to the penis of other branchiobdellidans.

There is no spermatheca, hence some form of hypodermic impregnation must occur, though no packets of spermatozoa have been observed on the dorsal surface of any specimen of any member of the genus. Such packets of spermatozoa have been reported by Holt (1949:549) in *Xironogiton instabilis* (Moore, 1894).

*Variations.*—In several of the specimens examined, the bursa lies along the dorso-ventral axis of segment VI, presumably compressed by a contraction of the body-wall. No other variations were noted.

*Affinities.*—*Ellisodrilus durbini* (Ellis, 1919) and *E. clitellatus* Holt, 1960, have dorsal ridges on some segments: on segment VIII in *E. clitellatus* and segments II–V and VII, VIII in *E. durbini*. *Ellisodrilus carron-*

*amus* lacks these ridges produced by supernumerary muscles (Holt 1960:171–172). *Ellisodrilus carronamus* further differs from its two congeners in its apparently larger size and somewhat larger and darker jaws with a dental formula of (?)5/5. The absence of dorsal ridges distinguishes *E. carronamus*.

There appears to be a north-south gradient in the distributions of these species with *E. carronamus* the southern-most and *E. durbini* to the north, in part at least, in areas scoured by the Pleistocene glaciations (Holt 1960:171; 174).

*Branchiobdellidan associates.*—*Ellisodrilus carronamus* shares its type locality with four other branchiobdellidans: *Cambarincola philadelphicus* (Leidy, 1851), *Xironodrilus formosus* Ellis, 1918, *Pterodrilus cedrus* Holt, 1968b, and *Oedipodrilus anisognathus*, newly described herein.

*Material examined.*—The types; six specimens taken from Roaring River on *Cambarus tenebrosus* Hay, 4.7 miles north of Rickman, Overton County, Tennessee, by Perry C. and Virgie F. Holt, 4 Jul 1958.

*Oedipodrilus anisognathus*, new species  
Fig. 3

*Type specimens.*—Holotype USNM 119534 and one paratype, USNM 119535 taken from a small stream on *Orconectes* sp. in Montgomery Bell State Park, Dickson County, Tennessee, by Perry C. and Virgie F. Holt, 4 Jul 1958; three paratypes, USNM 119536–119537 taken on *Orconectes* sp. from Carr Creek, about 3.0 miles south of Livingston, Overton County, Tennessee, by Perry C. and Virgie F. Holt, 26 Jul 1961.

*Diagnosis.*—Small worms (holotype 1.8 mm in length); lips entire; no oral papillae; no dorsal ridges; posterior segments markedly greater in diameter than anterior ones; jaws greatly dissimilar in size, upper one about  $\frac{1}{4}$  to  $\frac{1}{3}$  that of lower in length, dental formula 2/1; bursa relatively small,  $\frac{1}{2}$  body diameter in length; penis with (?) hooks; spermiducal gland lies longitudinally in coelom, with obscure deferent lobes; prostate

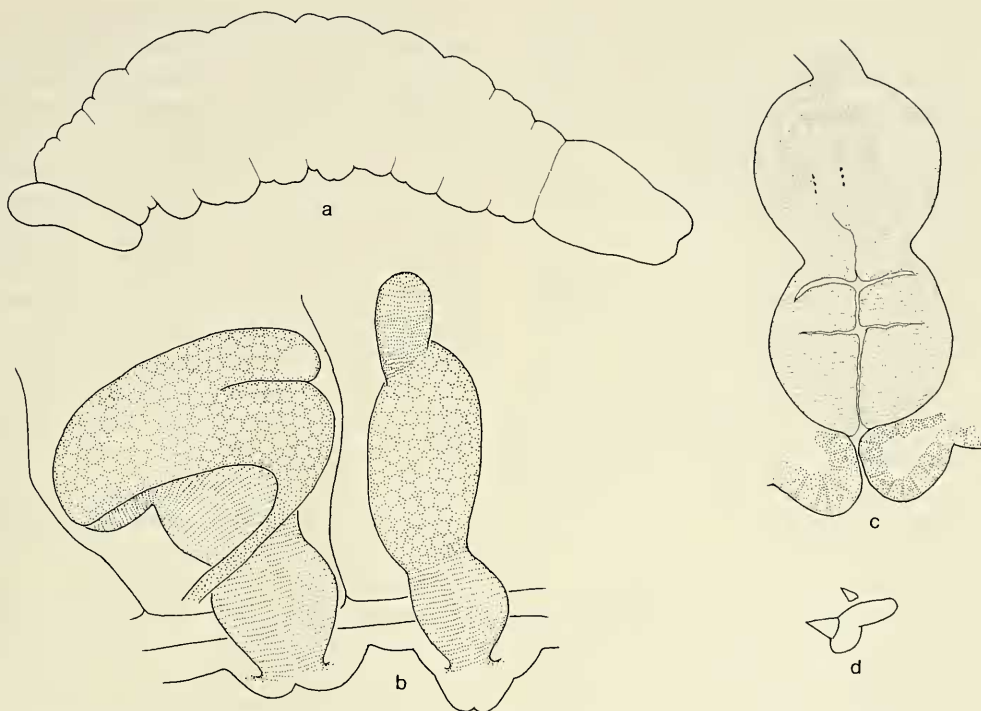


Fig. 3. *Oedipodrilus anisognathus*, holotype. a, Lateral view of entire animal; b, Lateral view of male efferent apparatus; c, Optical section of bursa; d, Lateral view of jaws.

with ectal end arising at about ental third of spermiducal gland, about  $\frac{1}{3}$  length of latter, with ental bulb; spermatheca with ectal bursa, cylindrical bulb, narrow ental process.

**Etymology.**—Greek: *anisos*, unequal; *gnathos*, jaw.

**Description.**—The specimens of *Oedipodrilus anisognathus* that constitute the type series have the following mean dimensions: total length, 1.4 mm; greatest diameter, 0.4 mm; head length, 0.4 mm; head diameter, 0.2 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.4 mm.

The worms have a somewhat corpulent appearance with slender heads. There are no supernumerary muscles of the prosomites of the body segments: the outline of the body is smooth. There is a slight constriction delimiting the peristomium; an internal pharyngeal sulcus lies at the greatest diameter of the head, often marked by a slight, shallow external one. The lips are

entire, the dorsal somewhat longer than the ventral one. No oral papillae are apparent.

The jaws are distinctive: unlike any others known for any member of the order. The upper jaw is small with two small, obscure teeth; the lower, three or four times the length of the upper, is massive, with flaring lateral flanges and a single, large, triangular tooth.

The spermiducal gland is proportionately small, as is the entire male reproductive system, and lies along the longitudinal axis of the body. Deferent lobes are not prominent. The prostate consists of a rather thick lobe of the spermiducal gland, about  $\frac{1}{3}$  the latter in length, with a clear ental bulb. It does not differ from the spermiducal gland in its histological appearance.

The bursa is an elongated ellipsoid with a shallow constriction separating its atrial and penial sheath portions. There is a somewhat irregular atrial fold. The penis is an elongated tube coiled inside the penial sheath,



attached only at the ectal end of the lumen of the latter and to its ental continuation as the ejaculatory duct. In its everted position the penis would be lined by a thin layer of tissue, possibly muscular. Penial hooks are few in number and difficult to detect with customary methods: there appear to be two or three pairs.

The ejaculatory duct is a short, thick muscular tube, almost as great in diameter as in length.

The ectal duct of the spermatheca is a short, thick, muscular spermathecal bursa. About  $\frac{1}{2}$  the total length of the spermatheca is composed of the spermatozoa storing bulb. There is a narrowed ental process with a thick muscular wall.

*Variations.*—None were noted in the available material.

*Affinities.*—Three other species of *Oedipodrilus* have been described: *O. oedipus* Holt, 1967, the type species from Humphreys County, Tennessee; *O. macbaini* (Holt, 1955), from Tennessee northward to Illinois and Pennsylvania; *O. cuetzalananae* Holt, 1984, from the state of Puebla, Mexico. *Oedipodrilus oedipus* has dorsal ridges, jaws with a  $5/4$  dental formula, a much shorter penis with many penial hooks and lacks an ental process of the spermatheca, differing from *O. anisognathus* in all these features. *Oedipodrilus macbaini* principally differs from *O. anisognathus* in the  $5/4$  dental formula, the much longer penial sheath and remarkably longer penis with many prominent hooks and the very long ectal duct of the spermatheca and the absence of a spermathecal ental process. *Oedipodrilus cuetzalananae* has a  $5/4$  dental formula; a very small, often obscure, prostate; a long, coiled penis with many hooks; a slender spermatheca with a long ectal duct, a thick-walled bulb and no ental process: *O. anisognathus* is different in all these features. Holt (1984: 40) said that “[t]he three known species of the genus form a coherent group and it is futile at this stage to speculate about which is more closely related to the other.” In general, this statement is still true, but perhaps

the unusual (? gill-clipping) jaws of *O. anisognathus* separates it more widely from the other species of the genus. Notice should be taken here of some similarities of these species with some members of the genus *Sathodrilus*, all of which likewise have an eversible penis. In most species of *Sathodrilus* the penis is a straight tube attached by strands of tissue to the inner wall of the penial sheath and everts as a membranous cup-shaped structure. But the penis of *S. villalobosi* Holt, 1968a, is an elongated tube with shallow coils (Holt 1984:40, fig. 3a) that, however, lacks penial hooks. These penial hooks may be the only character that reliably separates the two genera.

*Habitat.*—*Oedipodrilus anisognathus* has, though, not to as marked degree as some such species, the appearance of parasitic, gill-inhabiting worms: a thinner than usual body-wall, expanded posterior body segments, elongated and tapering head and peristomium. The jaws, closer in shape than are those of any other species to those of *Bdellodrilus illuminatus* Moore, 1895, which is known to inhabit the gill chambers of its hosts and to be parasitic, seem well suited to piercing the thin cuticle of the host's gills. More to the point, the gut of all the specimens examined of *O. anisognathus* is filled with a homogeneous coagulum, most likely blood, without any of the usual components of the slime found on the outer surfaces of the host. These worms most likely inhabit the gill chambers of the host.

*Hosts.*—*Orconectes juvenilis* (Hagen).

*Distribution.*—*Oedipodrilus anisognathus* is known only from the two localities cited: the type locality is in the Central (Nashville) Basin; the other in the eastern Highland Rim, the uplands surrounding the Nashville Basin.

*Oedipodrilus macbaini* (Holt, 1955)

Figs. 4, 5

*Cambarincola macbaini* (Holt 1955:27–31).  
*Oedipodrilus macbaini* (Holt 1969:205; 1984:39).

*Type specimens.*—Holotype, USNM 25952, six paratypes, PCH 134, taken from Charles Creek, eight miles west of Ashland on State Highway 5, Boyd County, Kentucky, on *Orconectes* sp. by Rodney MacBain, Jul 1948 (Holt 1955:29).

*Diagnosis* (emended).—Small- to medium-sized worms (average length of five specimens of type series and five specimens from Powell County, Kentucky, 1.8 mm); lips entire; no oral papillae; no dorsal ridges; jaws small, dental formula 5/4; bursa exceeds body diameter in length; penial sheath three to four times length of bursal atrium; penis long cuticular tube furnished with recurved hooks, coiled within lumen of penial sheath; ejaculatory duct proportionately short, thick, muscular; spermiducal gland about  $\frac{2}{3}$  body diameter in length, its diameter about  $\frac{1}{2}$  its length; prostate short, lying along ental third of spermiducal gland; non-differentiated, with ental bulb; spermatheca approximately equal to bursa and penial sheath in length, composed of long ectal duct, narrow median region, elongate bulb.

*Etymology.*—For the collector, Rodney G. MacBain.

*Description.*—Five specimens of the type series, collected in 70 percent ethanol have the following average dimensions: total length, 1.2 mm; greatest diameter, 0.3 mm; head length, 0.2 mm; head diameter, 0.1 mm; diameter, segment I, 0.1 mm; diameter, sucker, 0.2 mm (Holt 1955:27–28; modified to conform to current usage). In comparison, five specimens from Powell County, Kentucky, have the following average dimensions: total length, 2.4 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.3 mm. The discrepancies in these measurements probably result from differences in the fluids used in collecting; material taken since 1958 by Holt has been fixed in a solution composed of five parts of formalin to 95 parts of 70 percent ethanol. The latter fluid is far superior to ethanol alone, in part because

of a lesser degree of contraction of the animals.

The lips are entire; there are no oral papillae. There is one internal pharyngeal sulcus, but externally there is little indication (by an external sulcus) of its location. There are no supernumerary muscles of the dorsum of any body segments: the body outline is smooth.

The jaws present no distinctive features: they are small, delicate in appearance and light in color. The dental formula is 5/4. The gut is markedly narrowed in segments V and VI: most of the space in these segments is occupied by the spermatheca and male reproductive organs. Diatoms and detritus constitute the food found in the gut.

The anterior nephridiopore, undetectable in the entire specimens of the type series (Holt 1955:28) is, as determined by study of sectioned animals of the material from Powell County, Kentucky, a single minute opening on the dorsum of segment III.

The spermiducal gland is unremarkable, about twice its diameter in length and usually lying in a vertical position in the anterior portion of segment VI. The prostate, composed of cells similar to those of the spermiducal gland, is about  $\frac{1}{3}$  the diameter and length of the latter and arises entad to the junction of the spermiducal gland and ejaculatory duct (Fig. 4b). It has a small ental bulb in the Powell County animals which is not apparent in the paratypes. This discrepancy may be attributed to the contracted state of the latter.

The ejaculatory duct, as determined from sections (Fig. 5c) is a relatively short, thick and muscular tube distinctive only in the thickness of its inner layer of circular muscles.

The bursa is a very long, cylindrical tube that is variously bent as it courses dorso-laterad over the gut to its union with the ejaculatory duct. The bursal atrium is composed of a moderately thick inner layer of circular muscles and an outer thinner one of longitudinal (in reference to the organ) muscles and encloses what is actually the



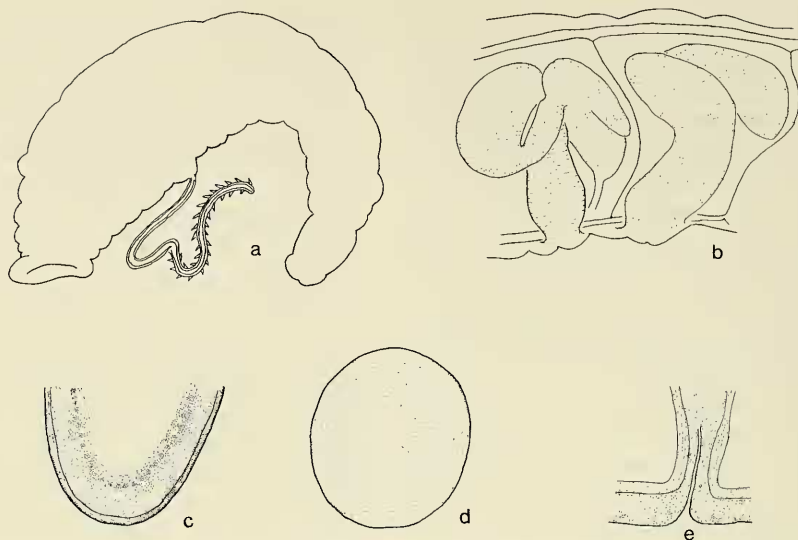


Fig. 4. *Oedipodrilus macbaini* (Holt, 1955), specimens from Powell County, Kentucky. a, Lateral view of entire animal with everted penis; b, Lateral view of reproductive systems (after Holt 1955); c, Section through ental end of spermathecal bulb; d, Cross section of ectal duct of spermatheca; e, Section through outlet pore of spermatheca.

portion of the penis that is not enclosed in the penial sheath in its retracted state (Fig. 5a). Most of the bursa consists of the penial sheath whose wall is apparently composed of the same, but much thinner layers as is the bursal atrium. Its capacious lumen contains the loops of the cuticular penis (Figs. 5b, c).

These dimensions of the bursa (atrium and penial sheath) accommodate the inordinately long cuticular penis. When completely everted the penis may actually be longer than the animal itself (Fig. 4a shows the penis much foreshortened). Retracted, the penis appears to consist of a thin layer of tissue with a cuticular lining. These layers are continuous with those composing the penial sheath and ejaculatory duct (Fig. 5a, b, d). When everted, the ectal portion of the penis is provided with recurved hooks (Figs. 4a, 5d, e) that lie within the lumen of the uneverted penis (Fig. 5d, e) which are absent from its ectal- and ental-most portions (Fig. 5a, b).

Such features of the penis, as might be expected, are matched by the structure which receives it in copulation: the spermatheca. There is a short ectal pore canal composed of the same layers as the body wall and the bursa (Fig. 4e) which passes shortly entad into the long and expanded ectal duct proper of the spermatheca (Fig. 4b, d, e). This duct courses dorsad, loops over the gut and is itself at least twice as long as the body diameter. The inner layer of the spermathecal duct is composed of cells with processes extending radially into the lumen of the duct (Fig. 4d). The spermatheca ends entally in a large, ventrally directed ovoid bulb.

*Affinities.*—See the discussion of the affinities of *O. anisognathus* above.

*Variations.*—The loops and bendings of the penial sheath and spermatheca take various positions within their segments. A careful comparison of paratypes with the other specimens herein assigned to the species lead to the conclusion that the differences in size and the apparent absence of

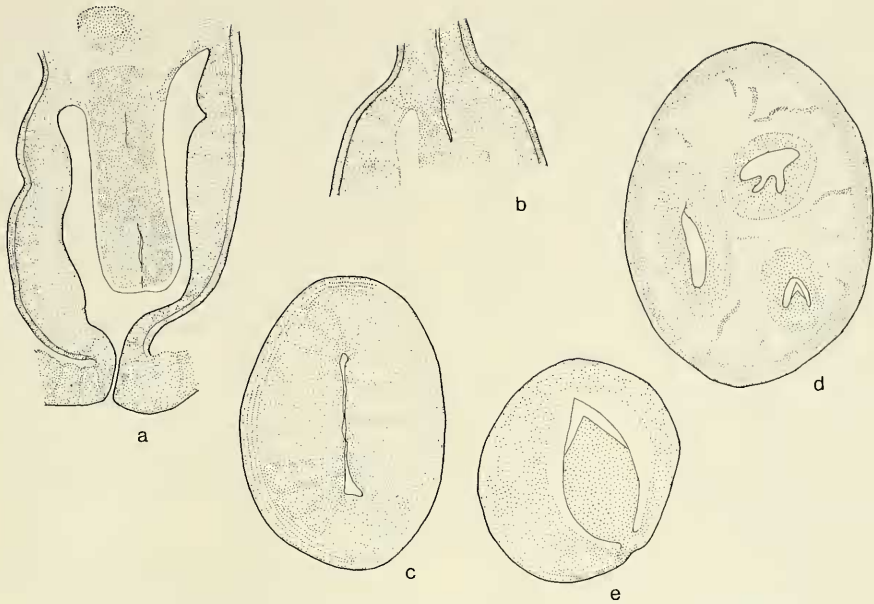


Fig. 5. *Oedipodrilus macbaini*, specimens from Powell County, Kentucky. a, Optical section through bursal atrium and ectal end of retracted penis; b, Optical section through ental end of penial sheath portion of bursa and penis; c, Optical cross section of ejaculatory duct; d, Optical cross section of penial sheath; e, Optical cross section of penis.

an ental bulb of the prostate in these type specimens is accounted for by the differences in fixation (see above).

*Hosts*.—See “Material Examined” below.

*Distribution*.—*Oedipodrilus macbaini* is widely dispersed throughout the Ohio River drainage in Tennessee, Kentucky, Ohio and Pennsylvania, and the Illinois River in Illinois. It is, therefore, a member of the diverse branchiobdellidan fauna that is derived from the pre-Pleistocene inhabitants of the Cumberland River and ultimately the ancient Teays drainages that has followed the retreating ice northward (Hobbs et al. 1967:69 et seq.; Holt 1968b:5, 1969:199).

*Material examined*.—(Unless otherwise noted all collections were taken by Perry C. and Virgie F. Holt). Illinois. Vermillion County, 9.2 miles north of Danville on U.S. Highway 136, on *Orconectes propinquus* (Girard), *O. virilis* (Hagen), *O. immunis*

(Hagen), 25 Jul 1958. Indiana. Montgomery County, 6.4 miles north of junction of Indiana highways 47 and 234, 24 Jul 1958, on unknown host, PCH 802; Orange County, 8.3 miles north of Crawford County line on Indiana Highway 145, 26 Jul 1958, on *Cambarus laevis* Faxon, *O. virilis*, PCH 812; Parke County, 5.6 miles west of Bellmore on U.S. Highway 36, 26 Jul 1958, on *O. immunis*, *O. propinquus*, PCH 807; Parke County, 4.2 miles north of Rockville on U.S. Highway 41, on unknown host, 26 Jul 1958, PCH 806; White County, 2.6 miles north of junction of U.S. highways 421 and 24 at Reynolds, 24 Jul 1958, on *O. virilis*, *O. propinquus*, PCH 801. Kentucky. Boyd County, 8 miles west of Ashland from Charles Creek on Kentucky Highway 5, Jul 1948, on *Orconectes* sp., R. G. MacBain, PCH 134. [Type locality]; Carter County, 1.9 miles northeast of Carter-Rowan County line on U.S. Highway 60, on unknown host,

23 Apr 1961, S. E. Neff and P. C. Holt, PCH 1360; Clarke County, 4.6 miles south of Winchester from Howard Creek on U.S. Highway 227, 30 Jul 1958, on *O. rusticus* (Girard), PCH 840; Fleming County, 1.5 miles northeast of Cowan on Kentucky Highway 32, on unknown host, 20 Apr 1961, S. E. Neff and P. C. Holt, PCH 1357; Harrison County, 0.5 mile northwest of Renaker on Kentucky Highway 36 from South Fork of Raven Creek, on *O. rusticus*, *C. b. bartonii*, 27 Jun 1964, J. F. Fitzpatrick, PCH 1788; Jackson County 1.8 miles south of junction of Kentucky Highway 30 and 1190, 29 Jul 1958, on *O. sp.*, PCH 831; Johnson County, 6 miles northeast of Paintsville on U.S. Highway 460, on *C. b. bartonii*, 6 Aug 1961, P. C. Holt, PCH 1454 (USNM 37799); Madison County, 9.3 miles north of Richmond on U.S. Highway 227, on unknown host, 30 Jul 1958, PCH 841 (USNM 37175); Nicholas County, at Meyers, on unknown host, 20 Apr 1961, S. E. Neff and P. C. Holt, PCH 1358; (USNM 37565); Powell County, 1.4 miles east of Slade on Kentucky Highway 11-15, on unknown host, 29 Jul 1958, PCH 836 (redescription based on this collection); Powell County, 4 miles northeast of Nada on Kentucky Highway 77, on unknown host, 30 Jul 1958, PCH 845. Ohio. Jefferson County, 4.2 miles northeast of Bloomingdale, on U.S. Highway 22, on *C. b. bartonii* and *O. obscurus* (Hagen), 7 Aug 1960, PCH 1226; Stark County, 3.8 miles west of Alliance on U.S. Highway 62, 3 Aug 1960, on *O. obscurus*, PCH 1205; Wayne County, 3.9 miles west of Riceland on U.S. Highway 30, on *O. propinquus*, 3 Aug 1960, PCH 1204; Williams County, 0.8 mile west of junction of U.S. highways 6 and 127, on *O. rusticus*, 3 Aug 1960, PCH 1201. Pennsylvania. Butler County, 4.6 miles northeast of crossing of Pennsylvania Highway 68 and Pennsylvania Turnpike near Zelienople, on *C. b. bartonii* and *O. obscurus*, 6 Aug 1960, PCH 1225; Butler County, Wolf Creek at crossing of Pennsylvania Highway 108, 4.9

miles northeast of Harlansburg, on *O. obscurus*, 6 Aug 1960, PCH 1224; Erie County, French Creek at junction of U.S. highways 6 and 19, on *O. obscurus*, 5 Aug 1960, PCH 1216; Erie County, 2.6 miles west of Union City on U.S. Highway 6, on *C. b. bartonii* and *O. obscurus*, 5 Aug 1960, PCH 1215. Tennessee. Putnam County on Tennessee Highway 56 at Baxter, on unknown host, 25 Jul 1961.

*Notes.*—The streams from which collections were taken by P. C. and V. F. Holt were all small- to medium-sized ones in which the hosts were taken by hand or with a dipnet. Most are in hilly, wooded country, but some (in Ohio) are in the plains on glacial silt.

The gut contents of *O. macbaini* include diatoms and the usual detritus that adheres to the exoskeleton of the hosts.

*Sathodrilus rivigeae*, new species

Fig. 6

*Type specimens.*—Holotype USNM 119545 and two paratypes, USNM 119546, [PCH 1089] taken from clear cool pools in a medium-sized stream in Ouachita National Forest, 3.2 miles east of Joplin, Montgomery County, Arkansas, at crossing of U.S. Highway 270, on *Orconectes palmeri longimanus* (Faxon) 23 Jun 1960, by Perry C. and Virgie F. Holt.

*Diagnosis.*—Medium-sized worms (holotype 2.8 mm in length); lips entire, peristomium demarcated by distinct sulcus; no oral papillae; no dorsal ridges of body segments; jaws small, delicate, in length  $\frac{1}{18}$  head length, dental formula (indeterminant in types) (?)  $1\frac{1}{4}$ ; bursa about  $\frac{1}{2}$  body diameter in length, constriction at mid-length marks junctions of bursal atrium and penial sheath; penis eversible, membranous, equal (when retracted) to penial sheath in length, atrial fold present; spermiducal gland large, about  $\frac{7}{11}$  body diameter in length, with large prominent deferent lobes; prostate subequal in diameter,  $\frac{3}{4}$  in length of spermiducal



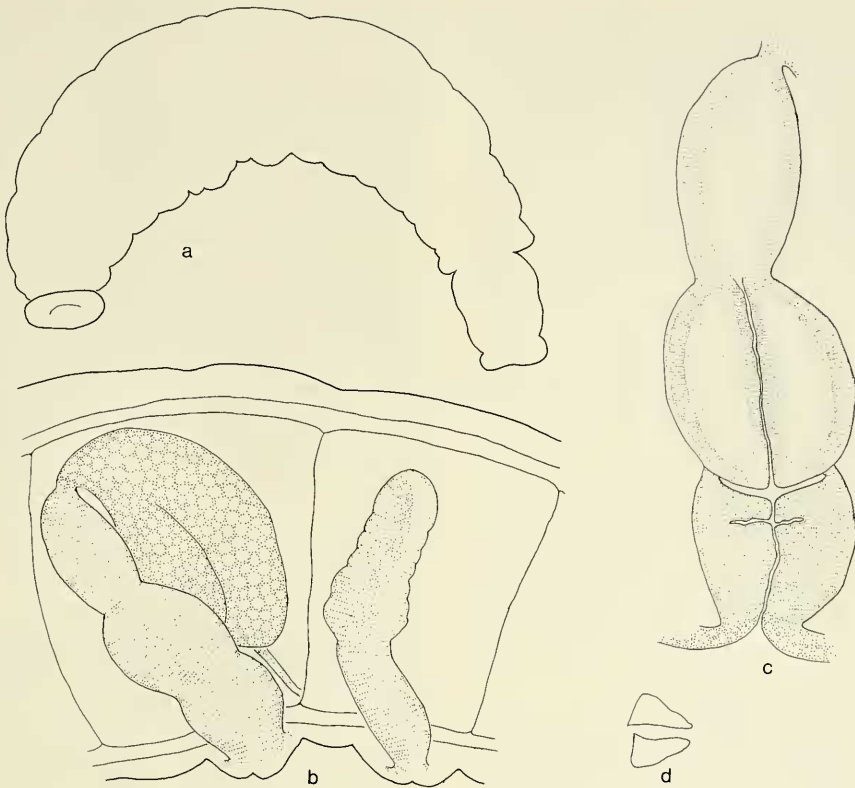


Fig. 6. *Sathodrilus rivigeae*, holotype. a, Lateral view of entire animal; b, Lateral view of reproductive systems; c, Optical section of bursal complex and ejaculatory duct; d, Lateral view of jaws.

gland, non-differentiated histologically; spermatheca with ectal duct, about  $\frac{1}{3}$  total length, bulb elongate ovate.

*Etymology*.—An anagram based on my co-collector's first name.

*Description*.—The paratypes are somewhat smaller than the holotype which has the following dimensions: total length, 2.8 mm; greatest diameter, 0.5 mm; head length, 0.4 mm; head diameter, 0.3 mm; diameter, segment I, 0.4 mm; diameter, sucker, 0.4 mm.

The lips lack lobes or tentacles, the peristomium is somewhat less in diameter than the greatest diameter of the head and a distinct annular sulcus separates it from the remainder of the head. The prominent internal pharyngeal sulcus is matched exter-

nally by a broad shallow one. Oral papillae are absent. There are no dorsal supernumerary segmental muscles: the body outline is smooth.

The jaws are difficult to interpret in the three available specimens: they are small and delicate in appearance, dark in color in the holotype, lighter in the paratypes and in one paratype the lower jaw appears to bear four teeth and the upper only one median tooth.

The spermiducal gland is of greatest diameter at the junction of the prominent deferent lobes and tapers gradually ectad to its union with the ejaculatory duct (the deferent lobes and ental portion of the gland are obscured in the illustration).

The prostate is unusually large among the

members of the genus. It arises from the spermiducal gland about a third of the length of the latter from its ectal end and extends entally to the junction of the deferent lobes. It appears to be composed of the same granular epithelium as the spermiducal gland: it is non-differentiated. There is no obvious ental bulb; but one paratype appears to have a short clear space between the investing peritoneum and its ental-most glandular cells.

The bursa is elongate with a broad and deep constriction at its mid-length at the union of the penial sheath and bursal atrium. The atrium has thick muscular walls and the atrial fold is thin and irregular. The penial sheath is lined by an epithelium (? muscular) and encloses the penis in a commodious cavity. The latter is an almost straight cuticular tube with minute longitudinal folds and is likewise covered with a layer of presumably muscular tissue.

The diameter of the ejaculatory duct is more than half its total length and its lumen is greatly expanded. It has the structure of a bulb whose function is that of a pump.

The spermatheca has a long ectal duct. Its bulb in the holotype is a thickened muscular elongate sac with a narrow lumen. Spermatozoa may be absent. The spermathecal bulbs of the paratypes are of the more common obovate type without ental processes.

*Variations.*—Two were noted (an unusual number among branchiobdellidans): the differences in the spermathecal bulbs just noted and in the contents of the gut. In the holotype the middle sacculations of the gut contain dark brown particles of unidentifiable detritus; the guts of the smaller paratypes are filled with a homogeneous clear material similar in appearance to that found in gill-inhabiting species; but the jaws are ill-adapted for clipping the gill filaments or piercing the articular membranes of the host.

*Affinities.*—Seven species of *Sathodrilus* have distinct prostates (as opposed to “prostatic protuberances” or “bulbs”). In all of these species the prostate arises from

the spermiducal gland entad to the junction of the latter with the ejaculatory duct. Of these, *S. dorfus* Holt 1977, *S. lobatus* Holt 1977, and *S. inversus* (Ellis, 1919) have ejaculatory ducts that are short and thickened (“bulb-like”) and are the closest known relatives of *S. rivigeae*. *Sathodrilus lobatus* has an expanded peristomium furnished with 14 lobes, its spermiducal gland and prostate are proportionately lesser in diameter than those of *S. rivigeae* and the spermatheca has a prominent medial bulb and long ental process (Holt 1977:122–124, fig. 3). Peristomial lobes are absent in *S. inversus*; the spermiducal gland is noticeably narrowed at its ectal end; the spermatheca has a median bulb and a long spermatozoa storing bulb without a muscular wall or ental process (Holt 1977:128–131, fig. 6, 1981:855). The spermiducal gland and prostate of *S. dorfus* are short and thick; the spermatheca is composed of a long ectal duct, a median bulb and an ental process (Holt 1977:120–121, fig. 2). All three of these species are inhabitants of the Pacific versant of the northwestern United States. *Sathodrilus rivigeae* differs from them most noticeably in the muscular wall of its spermathecal bulb and is, at least superficially, closest to *S. inversus*, from which it further differs in the short lobes of the peristomium and the frequent divergence of the prostate from the spermiducal gland (Holt 1977, fig. 7) found in the latter.

*Branchiobdellidan associates.*—*Cambarincola vitreus* Ellis, 1918, a species of *Cambarincola* that appears to be *C. heterognathus* Hoffman, 1963, and a widespread undescribed Ozarkian species of *Xironodrilus* Ellis, 1918.

*Host.*—*Orconectes palmeri longimanus*.

*Distribution.*—Known only from the type locality.

*Material examined.*—The types.

*Notes.*—Branchiobdellidan associates of two species have been given herein because the data were readily available; it should always be borne in mind that rarely is only

one species of branchiobdellidan found in any given locality.

The resemblances of *S. rivigeae* to its congeners of the Pacific northwest is another example of the homogeneity of the eastern and western branchiobdellidan faunas of North America, almost totally isolated now by the continental divide.

The expanded, bulb-like ejaculatory ducts of the species of *Sathodrilus* discussed herein should be further investigated. Function is difficult to infer from form alone, but it is probable that, in species with long, eversible penes and long spermathecal ectal ducts, that these expanded ejaculatory ducts aid in pumping spermatozoa into the spermathecal bulb.

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- Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061. Mailing address: 1308 Crestview Drive, Blacksburg, Virginia 24060.